Colonisation and spread of *Hieracium* spp in the South Island high country over 25 years

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We would like to gratefully acknowledge the leaseholders that allowed us on to their properties to remeasure vegetation in this study. In the interest of maintaining the lessees' privacy and professional working relationships in this area this report does not contain any information identifying individual lessees or their properties.

Executive summary

This report documents the invasion of three *Hieracium* species across the lower eastern South Island from the 1980s to the mid 2000s. We use data from 124 permanently-marked vegetation transects that were established on 27 properties in non-forest communities across Canterbury and Otago between 1982 and 1986 (first measurement). Each transect was 100 m long and comprised 50, square 0.25m^2 quadrats placed at two metre intervals. These were remeasured between 1993 and 1998 (second measurement), and again between 2005 and 2007 (third measurement). The number of transects on each property ranged between one and ten, and their elevations ranged between 370 m and 1880 m. They therefore covered a broad range of plant communities, including highly-modified lowland vegetation, with many exotic species, short-tussock grasslands with associated exotic and native intertussock species, native tall-tussock grasslands, and native alpine herbfield communities. Some of these areas have changed in tenure over the 25-years of monitoring.

We report on the invasion patterns of the three most abundant *Hieracium* species: *H. lepidulum, H. praealtum*, and *H. pilosella*. We investigated the changes that occurred in these species at two spatial scales: (1) landscape, between transect scale (colonisation) and (2) local, within-transect scale (changes in abundance and percent quadrat cover). We examined the relationships between these changes and measured environmental, ecological and tenure variables for the first and second measurements (first period) and for the second and third measurements (second period).

We found that all three *Hieracium* species have expanded their range and increased locally in the eastern South Island since the 1980s. Overall, our modelling results showed little difference between the important predictors at the two scales or between the two periods. Species interactions appear to have been a dominant factor in the pattern of *Hieracium* invasion. All three *Hieracium* species were more likely to colonise, and/or had higher rates of increase in abundance or percent quadrat cover, on transects where short-tussock (*Festuca novae-zelandiae*) was more abundant. Other studies have also shown short-tussock grasslands to be susceptible to invasion by *Hieracium*. Consistent with other studies, we found that *H.*

praealtum was less likely to colonise and increase in percent cover on transects that had been previously oversown. However, *H. lepidulum* showed faster rates of increase in abundance on transects that had been oversown. Of the three species, tenure was only a significant predictor for *H. lepidulum*, where it was more likely to colonise, and had higher rates of increase in abundance on, transects in pastoral tenure. Mean monthly precipitation was marginally negatively related to the colonisation and local spread of *H. lepidulum* and the rate of increase in percent cover of *H. praealtum.* These results suggest that that these species may be slower to establish in wetter areas. This has also been demonstrated elsewhere. The effect of solar radiation on *Hieracium* invasion differed among the species: *H. pilosella* increased in abundance at faster rates on sunnier slopes, but *H. lepidulum* increased in percent cover at faster rates on shadier slopes during the second period. This is likely to be due to inherent differences in the ecology of each species.

Each of the three *Hieracium* species appears to be responding to different environmental factors, which may be due to differences in their ecological tolerances, or because they are at different stages of invasion, or a combination of both. Overall, initial species composition of the invaded plant community appears to be a key factor determining invasion success and subsequent spread, with short-tussock grasslands being more susceptible to invasion. Tall-tussock (*Chionochloa* spp.) grasslands were susceptible to *H. lepidulum* invasion, which was more likely to colonise and increase locally where tall-tussocks were abundant during both periods. *H. pilosella* also increased in percent cover faster where tall-tussocks were abundant.

Our analysis of this large-scale, long-term dataset summarises the last 25-years of *Hieracium* invasion in the South Island high country. The analysis emphasises the importance of species interactions and initial composition in the spread of the three *Hieracium* species.

Key words: *Hieracium lepidulum*, *Hieracium pilosella*, *Hieracium praealtum*, tussock grasslands, hierarchical Bayesian models, vegetation change, Tenure Review

Introduction

The recent investigation into the outcomes of Tenure Review highlights the concern felt by many groups over the future of the conservation estate, and the high country in general (Parliamentary Commissioner for the Environment 2009). Tenure Review is the process by which high country pastoral leases are split up, with some areas going into freehold, and other areas being put in to conservation management. One key area of concern irrespective of tenure or tenure review is the spread of invasive species throughout the high country, particularly once grazing has been removed. Species within the genus *Hieracium* (Asteraceae) have spread rapidly over the last few decades and can seriously degrade the quality of both pasture and native-dominated tussock grasslands (Espie 2001). Although *Hieracium* species began increasing in the South Island high country in the 1950s, it was not until the 1980s that widespread concern about their spread became apparent (Connor 1992).

Three *Hieracium* species are widespread throughout South Island tussock grasslands: *H. lepidulum*, *H. pilosella* and *H. praealtum* (Duncan *et al.* 1997; Rose & Frampton 1999; Espie 2001). *H. pilosella* has been the focus of many studies, probably because it has been the most conspicuous and abundant species (Treskonova 1991; Rose *et al.* 1998; Johnstone *et al.* 1999). This species grows in flat rosettes that produce stolons to form large areas of dense mats, which can outcompete other vegetation and reduce other plants from establishing (Espie 2001). Some studies on *H. pilosella* have compared it to *H. praealtum*, which is thought to be more palatable (Treskonova 1991; Scott 2001). *H. lepidulum* has larger leaves than *H. pilosella* and *H. praealtum*, and it can only reproduce by seed (Espie 2001). There is some evidence that the flowers of *H. lepidulum* and *H. pilosella* may be susceptible to grazing (Espie 1994; Norton & Reid 2009).

Previous studies have shown that in general, *Hieracium* abundance for all species is lowest at both low and high elevations (Treskonova 1991; Duncan *et al.* 1997; Rose *et al.* 2004). Plant communities change considerably with elevation; at high elevations they are less-modified by human activities and are thus more intact in terms of native biodiversity, which may confer some resistance to invasion (Duncan *et al.* 1997). At lower elevations, grasslands show signs of greater agricultural inputs (e.g., Rose *et al.* 1998). High management inputs, including

fertiliser and seed oversowing of pastoral species, reduce the abundance of *H. pilosella* (Norton et al. 2006); this is likely to be due to competition from the oversown pastoral species (Scott 2001).

Fertiliser has been linked to declines in the abundance of *H. pilosella* (Scott *et al.* 1990; Scott 2001; Lamoureaux *et al.* 2003), albeit only weakly in some situations (Rose *et al.* 1998). Duncan et al. (1997) suggested that high soil moisture may result in low *Hieracium* abundance. Similarly, Rose et al. (1998) found areas with high precipitation to have lower cover of *H. pilosella*.

Short-tussock (*Festuca novae-zelandiae*) grasslands have been shown to be more susceptible to invasion by *Hieracium* compared to tall-tussock (*Chionochloa* spp.) grasslands (Treskonova 1991; Rose *et al.* 1998; Rose & Frampton 1999; Rose *et al.* 2004). This is thought to be because short-tussock grasslands are more open, and tall-tussocks form larger canopies, reducing the light available for *Hieracium* to establish (Rose & Frampton 1999). However, *H. lepidulum* is shade-tolerant and it is able to establish within beech forests (Wiser *et al.* 1998); thus, we may expect different behaviour from the different species.

Grazing disturbance results in more open grasslands, which may reduce the resistance of tall-tussock grasslands to invasion (Rose & Frampton 1999). Despite this, it appears that *Hieracium* does not require bare ground to colonise and can spread within existing vegetation and litter (Treskonova 1991; Rose *et al.* 1995; Johnstone *et al.* 1999; Rose *et al.* 2004). Further study is required to obtain an understanding of what will happen to the large areas of tall-tussock tussock grasslands now being retired from grazing through the Tenure Review process.

Here we provide the largest landscape-scale study of *Hieracium* invasion over 25 years across the lower eastern South Island of New Zealand. It is unique in that it is relatively long-term and encompasses vegetation change across a large range of plant communities, environmental and management conditions. We use data from 124 permanent vegetation transects on 27 properties that were measured three times between 1982 and 2007. We use these data to investigate the invasion patterns of the three most abundant *Hieracium* species: *H. lepidulum*, *H. pilosella* and *H. praealtum*, at two different spatial scales: between transects and within transects. To understand the drivers of *Hieracium* invasion at these two spatial

scales, we relate the colonisation and spread of *Hieracium* to the local environmental and ecological conditions. In addition, the transects occur on properties that represent areas in both conservation and pastoral tenure, allowing us to explicitly examine the effects of tenure on Hieracium invasion at different spatial scales.

We can make predictions about which variables may be important at the different scales from previous studies that have examined relationships between environmental variables and *Hieracium* cover and/or abundance (Treskonova 1991; Duncan *et al.* 1997; Rose *et al.* 1998; Rose & Frampton 1999; Rose *et al.* 2004; Norton *et al.* 2006). The few regional studies on *Hieracium* abundance and cover have either not explicitly tested for relationships between environmental variables and *Hieracium* colonisation or presence and/or have grouped all *Hieracium* species together (e.g., Treskonova 1991; Duncan *et al.* 1997), making it difficult for us to make predictions of colonisation between transects for our study. Based on the existing literature, we predict that *H. pilosella* will have increased in abundance and/or cover regardless of tenure. It will have increased most in short tussock grasslands, and in areas with low soil fertility and few oversown species, and in areas with high solar radiation and with low precipitation. We predict that *H. lepidulum* will have increased in abundance and/or cover regardless of tenure. It will have increased in abundance and/or cover most in areas of short-tussock grasslands and on shady slopes. We can make few predictions about relationships between *H. praealtum* and environmental variables due to the paucity of research on this species and its relationship with environmental variables, but we may expect it to have increased less in pastoral tenure, due to its due to its purportedly higher palatability.

Methods

Data collection

Permanently-marked vegetation transects (n=125) were established in non-forest plant communities across Canterbury and Otago in the South Island of New Zealand between 1982 and 1986 (first measurement). These were re-measured between

1993 and 1998 (second measurement) and again between 2005 and 2007 (third measurement) (Figure 1). There were between one and ten transects on each of 27 properties (Duncan *et al.* 2001) and the interval between the measurement of each transect ranged between seven and 15 years.

Each transect was 100 m long and comprised 50, square 0.25m2 quadrats placed at two metre intervals. Percent covers of bare ground and litter were estimated to the nearest five percent in each quadrat. At the first measurement the presence of each vascular plant species inside each quadrat, including overhanging vegetation, was recorded. At the second and third measurements, each species was recorded in one of six cover classes (<1%, 2-5%, 6-25%, 26-50%, 51-75%, 76-100%). At the third measurement, five soil samples were taken at regular 20 m intervals along each transect and then pooled. Samples were dried and analysed to obtain their cation exchange capacity, total base saturation, pH, calcium, phosphorus, potassium, sulphate sulphur, magnesium, sodium, and bulk density using standard techniques (New Zealand Labs, Kay & Hill 1998). The location of each transect was recorded using a GPS.

The 125 transects ranged in elevation between 370 m and 1880 m. They therefore covered a broad range of plant communities, including highly-modified lowland vegetation, with many exotic species, short-tussock grasslands with associated exotic and native intertussock species, native tall-tussock grasslands, and native alpine herbfield communities (Day & Buckley 2007).

The software ArcGIS 9.1 (ESRI 2005) was used to extract elevation, slope, aspect, and long-term average temperature and precipitation data from national spatial datasets at each transect location, using the GPS co-ordinates for the bottom pole of each transect. Elevation was extracted from a 25×25 m resolution digital elevation model (DEM) provided by Landcare Research, New Zealand. Slope and aspect surfaces were derived from the DEM data using spatial analysis functions in ArcGIS, from which values were subsequently extracted at the transect locations. Climate-related data were extracted from 500×500 m resolution interpolated climate surfaces provided by the National Institute of Water and Atmospheric Research (Wratt *et al.* 2006). Mean monthly temperature and mean monthly precipitation taken over thirty years at each transect location were used. An index of

solar radiation, which is the potential amount of radiation from the sun that a transect may receive, was calculated from latitude, aspect, and slope (Kaufmann & Weatherred 1982).

Several properties went through Tenure Review during the study period. At the first measurement, only 16 of the 125 transects were in conservation tenure, while 109 were in pastoral lease. At the second measurement there were 31 transects in conservation tenure. At the third measurement, 42 transects were in conservation tenure, and 83 were in pastoral lease (Land Information New Zealand and Department of Conservation records).

Data analysis

One of the 125 transects was omitted from all analyses, because it was in a bog and was an extreme outlier in soil conditions. This transect was in pastoral tenure throughout the study and none of the three *Hieracium* species were present at any measurement.

Response variables

We wanted to be able to test our predictions of the drivers of *Hieracium* spp invasion by explaining variation in the spread of each species among and within transects using the measured environmental variables. We also wanted to find out if the variables that were important for predicting spread were consistent over time. We therefore investigated invasion between the first and second measurements (first period) and between the second and third measurements (second period).

We modelled three different response variables against the same set of predictors: (1) colonisation of new transects, (2) rate of change in abundance within transects, and (3) mean rate of change in quadrat percent cover within transects. Colonisation was a binomial (0, 1) response of whether the transect had been colonised during the time period or not; transects where the species was already present were omitted. Extinctions from transects were ignored because these were rare events.

Rate of change in abundance during each period was calculated by first summing the number of occupied quadrats of each *Hieracium* species on each

transect at each measurement ('abundance'). The 'abundance' at the first measurement was then subtracted from the 'abundance' at the second measurement. Because the interval between measurements differed for each transect, we standardised the change in abundance to a rate of change per ten years by dividing by the time interval between measurements then multiplying the change in abundance by ten. This was repeated for the second period. For each species, transformations were applied to the rate of change in abundance and the data was rescaled to make it positive so that it could be log-transformed or a square-root transformed: we added four to the rate of change in abundance of *H. lepidulum* that was log-transformed, 17 was added to *H. pilosella* that was square-root transformed, and the rate of change in abundance of *H. praealtum* was not transformed.

We could not be sure that each quadrat on each transect was relocated precisely at each measurement because only the top and bottom of each transect was marked. Therefore, we calculated a rate of change in percent quadrat cover for each transect during the second period by first using the midpoint of the cover score values to estimate the percent quadrat cover of each *Hieracium* species on each transect at the second and third measurements (0.5, 3.5, 15.5, 38, 63, 88). The percent cover at the second measurement was subtracted from the percent cover at the third measurement. This change in percent cover was divide by the time interval between measurements then multiplied by ten, to give a rate of change in percent quadrat cover per ten years. The rate of change in percent cover did not need to be transformed in order to meet the normality assumption for any of the three species.

Predictor variables

There were a large number of potential explanatory variables and many of these were correlated, particularly the soil variables from the third measurement (Appendix 1). To reduce the number of soil variables we performed a principal components analysis (PCA) to examine the relationships among the soil variables for the 124 tussock grassland transects. A correlation matrix was specified in order to standardise the data (McCune & Grace 2002). Variables were transformed to meet the assumption of normality before being put in to the PCA: square-root of soil cation exchange capacity, log base saturation, square-root of calcium, log

magnesium, log potassium, log sodium, pH, log phosphorus, log sulphur, square-root of soil bulk density. The first two principal components were used as explanatory variables in subsequent analyses (see results). The PCA was run in R v. 2.9.1 (R Core Development Team 2009).

Given the changes in leaseholders on many properties over the study period, neither accurate grazing nor other detailed management information were available for all transects for the 25-year period. To avoid observer bias in grazing assessment we used a two-level categorical tenure variable as a coarse measure of management; transects in conservation tenure were in Department of Conservation management, and transects in pastoral tenure were in either pastoral lease or freehold. Dividing this variable in to finer categories was attempted but did not generate a tractable variable, as the categories became highly unbalanced and parameters could not be estimated in modelling.

We used the ratio of previously oversown species to non-oversown species ('oversowing') as an indication of pastoral management intensity. We collated a list of species that were likely to have been oversown in the high country over the past 50 years that were recorded on the transects, although we recognise that many of these are considered undesirable in many situations now: *Achillea millefolium, Agrostis capillaris, Arrhenatherum elatius, Cynosurus cristatus, Dactylis glomerata, Holcus lanatus, Lolium perenne, Lotus pedunculatus, Trifolium dubium, T. hybridum, T. pratense, T. repens* and *Vicia sativa* (Levy 1955; Keoghan & Allan 1992; Scott *et al.* 1995).

We calculated 'abundance' (number of quadrats present per transect) of tall-tussock (*Chionochloa* spp.) and short-tussock (*Festuca novae-zelandiae*) at the beginning of each period as an indication of initial species composition.

Based on our predictions laid out in the Introduction we selected eight variables that that we felt would best explain the observed patterns in *Hieracium* colonisation and spread and that would minimise collinearity (Table 1, Appendix 2): soil acidity (principal component axis 1), decreasing soil fertility (principal component axis 2), mean monthly precipitation, solar radiation, initial abundance of tall-tussock, short-tussock and oversowing for each period, and tenure at the beginning of the period considered. For each species, initial abundance at the

beginning of the period was used as a predictor in the rate of change in abundance models, and similarly initial percent cover was used as a predictor in the change in percent cover models. Continuous variables were standardised by their mean (McCune & Grace 2002). Because so few transects in conservation tenure were uncolonised by *H. praealtum* at the beginning of the study, we removed the tenure variable from the model of colonisation for this species.

Modelling Hieracium *colonisation and spread*

Because transects were nested within properties we constructed two-level, hierarchical Bayesian models (Gelman & Hill 2007) for the three response variables and each of the three *Hieracium* species, resulting in nine separate models in total. Because we had no *a priori* expectations for different relationships between response and predictor variables for different properties, we used varying intercept models only. We used non-informative priors for all parameters in all nine models (Gelman & Hill 2007). Because there were differences between the two time periods in how the richness and composition of the wider community changed during each period (Day & Buckley 2007), we entered time period in to the model as a fixed effect so that we could directly compare the effect of predictor variables on *Hieracium* change between the two time periods.

Colonisation was modelled as a Bernoulli process with a logit link function. Each dependent variable (y), colonisation, was modelled as a function of transect-level predictor variables, x. The transect-level model took the form $y_i \sim Bern(\alpha_j + \beta x_i)$, for $i = 1,\ldots, n_j$, where y_i is the colonisation of *Hieracium* sp, in the i^{th} transect, α_j is the regression intercept for the j^{th} property, β is the matrix of coefficients for the transect-level predictors, and n is the total number of transects. Because the value of several predictors, such as oversowing, tall-tussock abundance, short-tussock abundance and tenure, changed between measurement times we included the interaction between these variables and time period to account for this; thus the β values for these variables are the coefficients for these interactions. This resulted in a separate coefficient estimate for each variable in each time period. The hierarchical model treats the transect-level intercept terms, α, as though they come from a normal distribution across properties and models them as $\alpha_j \sim N(\gamma, \sigma^2_\alpha)$, for $j =$

1,…, J, where γ is the overall regression intercept term and σ^2_α is the property-level regression error, and J is the total number of properties.

Rate of change in abundance and percent cover were modelled as Gaussian processes with an identity link function. Each dependent variable (y) was modelled as a function of the same set of transect-level predictor variables and interactions with time period as above, x. In this case, the transect-level model took the form $y_i \sim N(\alpha_j + \beta x_i, \sigma^2_y)$, for $i = 1,\ldots, n_j$, where y_i is the rate of change in abundance or percent cover of the i^{th} transect, α_j is the regression intercept for the j^{th} property, β is the matrix of coefficients for the transect-level predictors, σ^2_y is the transect-level regression error, and n is the total number of transects. As for the previous set of models, the hierarchical model treats the transect-level intercept terms, α, as though they come from a normal distribution across properties and models them as $\alpha_j \sim N(\gamma, \sigma^2_\alpha)$, for $j = 1,\ldots, J$, where γ is the property level regression intercept and σ^2_α is the property-level regression error, and J is the total number of properties. Four transects were omitted from the analysis of change in percent cover due to missing data at the second measurement.

Models were fit using Markov Chain Monte Carlo iterations using Open Bugs (Thomas *et al.* 2006) called through the BRugs package of R version 2.9.1 (R Core Development Team 2009). Three simultaneously running Markov chains of at least 100,000 iterations were thinned at every 50th value to reduce the effects of autocorrelation on parameter estimates, with a 20,000-iteration burn-in. We visually assessed model convergence using the chain histories. Although Bayesian modelling does not generate P-values in the same way as Frequentist statistical method, predictors were considered to be 'significant' if their credible interval did not overlap zero. Because this analysis is iterative, if a credible interval is close to overlapping zero we considered the variable to be 'marginally influential'. Fully conditional models that included all predictors were taken as the final result in all cases because methods for determining the importance of predictor variables, model comparison, and model reduction using hierarchical Bayesian methods are still controversial (Gelman & Hill 2007).

Results

Data reduction

The PCA on the environmental variables reduced the ten soil variables down to two principal component axes that accounted for 71% of the variation (Table 2). The first principal component reflected a soil acidity gradient: declining logarithm of base saturation, square-root of calcium, pH, logarithm of potassium and logarithm of magnesium. The second principal component reflected a soil fertility gradient: decreasing cation exchange capacity, logarithm of sodium, logarithm of magnesium, and increasing bulk density. These axes were used in subsequent analyses as 'soil acidity and 'soil fertility' variables.

Patterns of change in Hieracium *spp*

The general trends for each *Hieracium* sp at each scale of the study can be described based on Figure 2. Overall, all three *Hieracium* species colonised transects and increased in abundance and percent quadrat cover over both periods, although *H. praealtum* showed a shallower rate of increase (Figure 2). *H. pilosella* and *H. lepidulum* colonised a similar number of transects over time, but *H. pilosella* was present on more transects throughout the study (Figure 2a). *H. pilosella* showed a high rate of increase in abundance during the first period (Figure 2b).

H. pilosella and *H. praealtum* occurred on a similar number of transects and were at a similar abundance at the first measurement. However, *H. pilosella* colonised more transects and increased in abundance at a faster rate than *H. praealtum* during both periods (Figure 2a, b). Compared to *H. pilosella*, *H. lepidulum* occurred on fewer transects, and was less abundant initially, but showed a similar trend of increase over time (Figure 2a, b). Overall, *H. lepidulum* colonised 45 transects, whereas *H. pilosella* only colonised 40 transects during the study.

At the second measurement, *H. pilosella* was at higher percent cover compared to the other two species and continued to increase in percent cover over time (Figure 2c). *H. lepidulum* also increased in percent cover over time, while the increase in *H. praealtum* was only marginal (Figure 2c).

Patterns of change in* Hieracium *spp in relation to tenure

The general trends for each *Hieracium* sp at each scale of the study within the two tenure categories can be described based on Figure 3. *H. pilosella* and *H. lepidulum* increased at all scales over both periods regardless of tenure (Figure 3). *H. pilosella* increased in abundance and percent cover at a greater rate in conservation tenure compared to pastoral tenure (Figure 3c, e). *H. lepidulum* colonised a large proportion of transects in conservation tenure during the second period (Figure 3a). *H. praealtum* did not colonise or spread at a great rate on either tenure and actually remained on the same number of transects overall in conservation tenure (Figure 3a).

Using tenure at the first measurement, *H. lepidulum* was not present on any transects in conservation tenure at the first measurement but was on almost half of all transects in conservation tenure by the third measurement (Figure 3a). *H. pilosella* was already present on most transects in conservation tenure at the first measurement, but continued to colonise more transects during the study (Figure 3a). *H. praealtum* was also present on most transects in conservation tenure initially, and colonised new transects during the first period but then went extinct from transects during the second period, so that it was on the same proportion of transects in conservation tenure at the third measurement as it was at the first measurement (Figure 3a).

The three species were present on a similar proportion of transects in pastoral tenure at the first measurement. *H. pilosella* and *H. lepidulum* colonised a similar proportion of transects in pastoral tenure over both periods (Figure 3b). The rate of colonisation by *H. praealtum* in pastoral tenure was slower than that of the other two species (Figure 3b).

H. pilosella and *H. praealtum* were more abundant on transects in conservation tenure compared to pastoral tenure (Figure 3). *H. pilosella* increased in abundance in both tenure categories during both periods (Figure 3c, d). *H. lepidulum* increased in abundance in both conservation and pastoral tenure during both periods, but it was at very low abundance in conservation tenure because it was not present on many transects in conservation tenure at the first measurement (Figure 2a). *H. praealtum* also increased in abundance in both tenure categories during both

periods, although this increase was only marginal during the second period in both tenure categories (Figure 3c, d).

H. pilosella had the highest percent cover in both conservation and pastoral tenure during the second period (Figure 3e, f). In conservation tenure, *H. praealtum* had a slightly higher percent cover than *H. lepidulum*. In pastoral tenure *H. lepidulum* had slightly higher percent cover than *H. praealtum*, and they increased at a similar rate (Figure 3e, f).

Relating patterns of change to environmental variables

Hierarchical Bayesian modelling showed that, as predicted, the measured environmental variables were able to predict the colonisation and spread of all three *Hieracium* species during the 25 year study period.

Colonisation

During both periods, *H. lepidulum* was significantly more likely to colonise transects that had high abundance of short-tussocks, high abundance of tall-tussocks, and were in pastoral tenure (Figure 4a). Mean monthly precipitation and soil acidity were marginally influential; *H. lepidulum* was more likely to colonise where precipitation was high, and where soils were more acidic (Figure 4a).

During both periods, *H. pilosella* was significantly more likely to colonise transects that had high abundance of short-tussocks (Figure 4b). During both periods, *H. praealtum* was significantly more likely to colonise transects that had high abundance of short-tussocks (Figure 4c). During the first period, *H. praealtum* was significantly less likely to colonise transects with high oversowing (Figure 4c).

Rates of change in abundance

During both periods, *H. lepidulum* showed significantly greater rates of change in abundance on transects where it was already abundant and where short-tussocks were abundant (Figure 5a). During the second period, H. lepidulum changed in abundance at a greater rate on transects in pastoral tenure or had high abundance of tall-tussock. Tall-tussock abundance was also marginally influential during the first period (Figure 5a).

During the first period, *H. pilosella* changed in abundance at a greater rate on transects that had high initial abundance of *H. pilosella* and high short-tussock abundance, but these were not significant during the second period (Figure 5b). The effect of solar radiation was marginally significant; H. pilosella changed in abundance at greater rates on transects with high solar radiation (Figure 5b).

None of the measured variables were significant for explaining the rate of change in abundance of H. praealtum during either period. The effects of initial H. praealtum abundance and short-tussock abundance were marginally influential; H. praealtum changed in abundance at a greater rate on transects where it was initially low in abundance and where short-tussocks were high in abundance (Figure 5c).

Rates of change in percent quadrat cover during the second time period

During the second period, *H. lepidulum* increased in percent quadrat cover significantly faster on transects where it was initially high in percent cover, on transects with high tall-tussock abundance and with low solar radiation (Figure 6a). The effects of precipitation was marginally influential; *H. lepidulum* showed a faster rate of change in percent cover where precipitation was low (Figure 6a).

H. pilosella changed in percent cover at a significantly faster rate on transects with high tall-tussock abundance (Figure 6b). *H. praealtum* increased in percent quadrat cover at a greater rate on transects with low precipitation (Figure 6c). The effects of oversowing and short-tussock abundance were marginally influential; *H. praealtum* changed in percent cover at a faster rate on transects with low oversowing and with high short-tussock abundance (Figure 6c).

Discussion

Here, we provided the largest landscape-scale study of *Hieracium* invasion in the south eastern South Island using a dataset that encompasses vegetation change over 25 years across the lower eastern South Island. It is unique in that it is relatively long-term, tracking vegetation change across a large range of plant communities, environmental and management conditions. The results show that invasion of these three *Hieracium* species has continued to occur over the past 25 years across the study area. While this study can show us general trends of invasion across the high

country, we cannot use it to conclusively determine the causal processes underlying these patterns of *Hieracium* invasion. This is because at this scale many environmental and management variables were correlated, making it difficult to determine the exact mechanisms behind these patterns. This study has, however, documented the trends in *Hieracium* invasion over a large area. Some of the relationships between *Hieracium* and environmental variables we found have also been observed in smaller-scale experimental studies.

This study examined the spread over 25 years of *Hieracium lepidulum*, *H. pilosella* and *H. praealtum* at two different scales: colonisation of transects measured change at a landscape scale, whereas changes in abundance and percent cover quantify change at the local, within-transect scale. Overall, our modelling results showed little difference between the apparent drivers at the two scales.

For most of the models, variables that were significant during the first period were also usually significant or marginally influential during the second period, indicating that the same processes are likely to have driven the changes in *Hieracium* at these scales over the 25 year study period. The widespread increase in *Hieracium* is therefore unlikely to be due to factors that have changed over the study period, such as fluctuating rabbit numbers (Parkes *et al.* 2002) or the removal of subsidies for farmers (see Johnstone *et al.* 1999).

Which environmental variables predict the colonisation and spread of the three* Hieracium *species?

The main conclusion from the results in this study is that initial conditions are key determinants of *Hieracium* invasion. This conclusion is consistent with other studies in tussock grasslands (Treskonova 1991; Espie 2001; Meurk *et al.* 2002; Rose *et al.* 2004). The abundance of short- and tall-tussocks represent different initial plant species composition because these species are associated with different intertussock species (Wardle 1991; Day & Buckley 2007). The positive relationship between short-tussock abundance and the colonisation and spread of *Hieracium* is likely to be a reflection of the open structure and composition of short-tussock grasslands, which makes them more susceptible to invasion (Rose *et al.* 1998). *H. lepidulum* and *H. pilosella* were also able to spread in tall-tussock grasslands, indicating that these

communities are not necessarily resistant to invasion by *Hieracium*. The contrasting effect of oversowing on the invasion of *H. lepidulum* and *H. praealtum* may reflect differences in ecological tolerances but again emphasises that *Hieracium* invasion will differ according to initial conditions at a given site.

Consistent with previous work, our results show that *Hieracium* was more likely to colonise and/or spread on transects in short-tussock grasslands (Figures 4, 5 and 6). Long-term studies in Marlborough and Otago have shown short-tussock grasslands to be more susceptible to invasion, due to their composition and structure (Rose *et al.* 1998; Rose & Frampton 1999; Rose *et al.* 2004; Diez *et al.* 2009). This resistance to invasion may be reduced when tussocks are grazed because the tussock canopy is reduced (Rose & Platt 1992; Diez *et al.* 2009). Burning significantly reduces the stature and reproduction of tussocks, as well as modifying surrounding species composition which may facilitate invasion of exotic species (Lee *et al.* 1993; Espie & Barratt 2006). However, because we were unable to gain an accurate measure of burning history on the transects in this study it is not possible to infer its role here.

The influence of solar radiation on *Hieracium* invasion differed among the species: *H. pilosella* increased in abundance at faster rates on sunnier slopes (Figure 5b), but *H. lepidulum* increased percent cover faster on shadier slopes (Figure 6a). Previous studies have also shown that shady slopes are more likely to be invaded by *H. lepidulum* (Rose *et al.* 2004), indicating that these differences reflect differing ecological preferences between the two species. Indeed, *H. lepidulum* is also a notable invader of beech forest (Wiser *et al.* 1998).

The literature suggests that the dense canopy and litter cover by tall-tussocks reduces invasion by *Hieracium* because it is shade-intolerant (Rose & Frampton 1999; Meurk *et al.* 2002). However, we found that both *H. lepidulum* and *H. pilosella* were able to increase in tall-tussock grasslands (Figures 4, 5 and 6). The shade tolerance of *H. lepidulum* can account for its increase in tall-tussock grasslands. However, the possible mechanisms behind invasion of these areas by the less shade-tolerant *H. pilosella* is unclear.

Areas with abundant tall-tussock cover produce high water yields (Mark & Dickinson 2008). This indicates that although *H. lepidulum* was less likely to colonise

and spread in areas with high precipitation, its positive increase where tall-tussocks were abundant may mean that it is tolerant of wetter areas. In contrast, *H. praealtum* had lower rates of spread in areas with high precipitation and were not related to tall-tussock abundance, so this species is probably less capable of increasing in wet areas (Duncan *et al.* 1997; Rose *et al.* 1998). *H. pilosella* has also been shown to be at low abundance in areas with high soil moisture (Rose *et al.* 1998). There is evidence here to suggest that environmental conditions created by tall-tussocks allow *H. lepidulum* and *H. pilosella* spread (Figure 4a, 5a, 6a).

The results suggest that *H. lepidulum* invasion may be favoured by pastoral management practises because it increased both in pastoral tenure and where oversowing was high (Figures 4a and 5a). In contrast, *H. praealtum* was less likely to colonise and spread where oversowing was high (Figures 4c and 6c), again possibly reflecting differences in the ecological tolerances of these two species. *H. lepidulum*'s greater rate of change in abundance on transects with high oversowing was surprising because other studies have demonstrated that pasture species can outcompete *Hieracium* spp., especially where fertiliser is applied. This has been demonstrated for *H. pilosella* in New Zealand (Scott *et al.* 1990; Scott 2001) and *H. floribundum* in Canada (Reader & Watt 1981; Reader 1990). It is possible that *H. lepidulum* is more competitive in pastoral environments, although recent studies do not support this (Radford *et al.* 2006; Radford *et al.* 2007; Radford *et al.* in press). In this dataset, transects at low elevations had higher oversowing (Appendix 1, R=-0.43). Relationships between elevation and the abundance of *Hieracium* observed elsewhere (e.g., Treskonova 1991; Duncan *et al.* 1997) may have been driven by differences in environment, management and species composition at different elevations.

H. lepidulum was more likely to colonise and spread in pastoral tenure but the invasion of *H. pilosella* or *H. praealtum* was not related to tenure (Figures 4, 5 and 6). Few studies have shown consistent changes in *Hieracium* spp. in relation to grazing removal (Rose & Frampton 1999; Mark & Dickinson 2003; Rose & Frampton 2007); however, in this case, tenure may not represent a clear distinction in land management strategies. Some transects in pastoral tenure had not been grazed for some time (lessees, pers. comm.), and there were obvious signs of sheep camps near

some transects in conservation tenure (N. Day, pers. obs.). In addition, grazing concessions are sometimes made during the tenure review process which allow restricted grazing on conservation land (S. Urlich, pers. comm., Parliamentary Commissioner for the Environment 2009).

We found that in this dataset only a narrow range of community types were represented within the conservation estate (Day & Buckley 2007). Relatively few transects were classified as conservation tenure and those that were, were more often tall-tussock grasslands (Table 3). This narrow representation was highlighted in the recent report on Tenure Review: *"The general outcome of tenure reviews to date is that the relatively productive lower altitude terraces, fans and basins have been transferred to unencumbered freehold title, while the colder, steeper, higher altitude tussock grasslands have become public conservation land"* (Parliamentary Commissioner for the Environment 2009: 34).

The differences observed among the *Hieracium* species in relation to tenure may be related to differences in initial species composition or environmental differences in each tenure category, rather than differences in grazing or land management (Table 3). We also found tenure to be highly correlated with rock type, with most transects in conservation tenure falling on greywacke rock (Appendix 3).

Given the high representation of tall-tussock grasslands in conservation tenure in this dataset, and the ability of *H. lepidulum* to invade tall-tussock grasslands, it is possible that *H. lepidulum* will continue to increase in areas of conservation tenure in the future. However, vegetation change in tussock grasslands can take many decades to become apparent (e.g., Mark & Dickinson 2003; Rose *et al.* 2004). Therefore the future composition of transects in conservation and pastoral tenure and the effects of invasion by *Hieracium* may not become apparent for several more decades.

Differences among* Hieracium *spp in their spatial and temporal patterns of spread

Overall, *H. pilosella* occurred on more transects, was more abundant, and had higher percent cover compared to *H. lepidulum* and *H. praealtum* throughout the study (Figure 2). The spread of *H. pilosella* has been a concern in tussock grasslands since the 1980s (Connor 1992), and it was already abundant when the transects in the

present study were initially established (Figure 2). Being wind-dispersed, *H. pilosella* is capable of producing a dense propagule rain. This, coupled with the fact that *H. pilosella* has the ability to establish and then continue to spread locally in a wide range of environments and vegetation types (Treskonova 1991; Rose & Frampton 1999; Meurk *et al.* 2002), enabled *H. pilosella* to increase at both scales within this study. Furthermore, it seems to be showing little sign of slowing down.

At the beginning of the study, *H. praealtum* occupied a similar number of transects, and was at a similar average abundance to *H. pilosella*, but its dynamics over time were quite different. The relative palatability of *H. praealtum* compared to *H. pilosella* may account for these differences in invasion dynamics (Hughes 1975; Scott *et al.* 1990; Treskonova 1991). An experimental study showed that while *H. praealtum* was relatively unaffected by simulated grazing, *H. pilosella* increased the number and length of its stolons (Makepeace 1985), suggesting that *H. praealtum* is a less aggressive invader.

Interestingly, *H. lepidulum* showed similar rates of increase to *H. pilosella* over both periods in the study; however, it was on fewer transects and was less abundant at the beginning and during the study (Figure 2a, b). *H. lepidulum* does not produce stolons, and can only reproduce by seed (Espie 2001). This means that it is less likely to form dense patches and exclude other plants from establishing in the same way that *H. pilosella* does (Espie 2001; Lamoureaux *et al.* 2003), but may only slow the rate of invasion and saturation of the landscape, not prevent it. The consistently low abundance and percent cover of *H. lepidulum* on transects in conservation tenure is accounted for by its absence on these transects at the first measurement. However, this species did colonise and continue to increase on transects in conservation tenure over the study period (Figure 3).

H. lepidulum may have experienced a longer lag-time in its invasion than *H. pilosella* that can last years or even decades (Radosevich *et al.* 2003). In these early stages of invasion, *H. lepidulum* may only establish and spread within its optimal environmental range. This may explain why the colonisation and spread of *H. lepidulum* was related to many environmental and ecological variables (Figures 4a, 5a, 6a).

***Implications for the spread of* H. lepidulum**

The aim of this study was to document the spread of *Hieracium* over the landscape and locally within transects. Distances between transects in this study were large, making it difficult to investigate smaller-scale relationships between source and sink populations. We found that *H. lepidulum* may have experienced a longer lag-time in its invasion than *H. pilosella* that can last years or even decades (Radosevich *et al.* 2003). In these early stages of invasion, *H. lepidulum* may only establish and spread within its optimal environmental range. As its populations continue to increase, propagule pressure on surrounding areas will increase, enabling it to establish and spread to areas that do not represent its optimal environmental conditions. These same dynamics may explain why *H. pilosella* has continued to increase overall during the study, and why few variables were able to predict its increase, while many variables could predict the colonisation and spread of *H. lepidulum*. In the long-term, *H. lepidulum* may become as widespread and abundant as *H. pilosella*.

It is possible that the lag in the spread of *H. lepidulum* may be related to below-ground processes. Both *H. pilosella* and *H. lepidulum* have greater biomass when their roots are involved in symbiotic associations with fungi, in the form of arbuscular mycorrhizal fungi (AMF), which allows more efficient uptake of soil nutrients (van der Heijden *et al.* 1998; Downs & Radford 2005). Indeed, AMF associations have been shown to be important in the invasion of other invasive Asteraceae, for example, *Centaurea maculosa*, in North America (Callaway *et al.* 2004). Shoot growth of *H. pilosella* differs according to the AM fungal symbiont (van der Heijden *et al.* 1998), and the AMF species present in the soil can change over time (Hart *et al.* 2003). The initial establishment of *H. pilosella* at sites could encourage the growth of AMF species that can facilitate the establishment and growth of *H. lepidulum*. This may help to explain the lag in the invasion by *H. lepidulum*, if it is limited in at least part of its range to a greater degree than *H. pilosella* by mycorrhizal interactions. An experimental study that found *H. lepidulum* to be overall a poorer competitor compared with its co-occurring species considered AMF as a possible explanation for its successful invasion in the field (Radford *et al.* 2007). Further investigation in to these ideas would be worthwhile.

Potential consequences of changing land use on* Hieracium *spread following Tenure Review

So far, properties that have been through tenure review have generally resulted in a narrow range of vegetation types being represented in the conservation estate; high altitude, relatively undisturbed plant communities such as tall-tussock grasslands are relatively represented more than low altitude areas (Parliamentary Commissioner for the Environment 2009). Although transects in conservation tenure in this study were not at higher elevations compared to those in pastoral tenure, the abundance of tall-tussocks were higher in conservation tenure compared to short-tussock abundance (Table 3).

We consider initial species composition at sites to be a key factor determining the patterns in the colonisation and spread of *Hieracium* observed in this study; less disturbed tall-tussock grasslands are apparently less-susceptible to *Hieracium* invasion (Rose & Frampton 1999; Meurk *et al.* 2002). However, the recent increase in *H. lepidulum*, and the continued increase of the already-widespread *H. pilosella*, means that we should still be concerned about ongoing *Hieracium* spread. In particular, the canopy created by tall-tussocks in areas in conservation tenure may not be adequate to resist invasion by *H. lepidulum* because it is shade-tolerant (Wiser *et al.* 1998; Espie 2001).

Although we cannot predict the impacts of continued *H. lepidulum* increase on plant communities or biodiversity, species within this genus can degrade the quality of both native and pastoral grasslands (Treskonova 1991; Wilson & Callihan 1999; Espie 2001). In addition, species within the *Hieracium* genus are considered invasive in many parts of the world, including Australia (Williams & Holland 2007) and North America (Wilson & Callihan 1999), suggesting that more research is needed on the processes driving the spread of these species.

If recommendations from the recent report on Tenure Review produced by the Parliamentary Commissioner for the Environment are followed, then the Department of Conservation will be responsible for administering a more diverse range of plant communities (Parliamentary Commissioner for the Environment 2009). This could lead to more disturbed and invasion-susceptible short-tussock grasslands being put in to conservation management. Norton et al. (2006) point out

that managing short-tussock grasslands is somewhat of a 'conundrum' because passive management, and the subsequent invasion by *Hieracium*, leads to declines in production, as well as declines in native biodiversity. Fertiliser and oversowing are only practical for reducing the spread of *Hieracium* in pastoral areas, because native biodiversity does not benefit from the large increases in introduced species (Norton *et al.* 2006).

Conclusions

We found that all three *Hieracium* species have both expanded their range and increased locally across the eastern South Island since the 1980s. These changes appear to be strongly related to initial conditions and composition. In addition, the three species appear to be responding to different environmental factors, which may be due to inherent differences in ecological tolerances, because they are at different stages of invasion, or a combination of both.

Due to the scale of this study and the wide range of environmental, management and plant communities represented in this study it is difficult to predict potential future changes that may occur in these *Hieracium* populations and the impacts they may have on future composition of tussock grasslands. Changes in composition in tussock grassland communities can take many decades to become apparent. We found evidence for relationships between increases in *Hieracium* and environmental, ecological and management variables, but we cannot determine the processes underlying these patterns with this large-scale correlative study. The difficulty of predicting future changes in *Hieracium* populations at the landscape scale is further hindered by the fact that this is the only data set of its type within New Zealand. We have documented the invasion patterns that have occurred over a large geographic area and highlighted areas where further research could be focussed in order to determine the underlying mechanisms behind the observed patterns of invasion.

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Cover photo: Alice Webster

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Table 1: List of variables used in the analyses including a description of how each was obtained and, in the case of predictor variables, which other of the many possible predictors they were highly correlated with.

Variable name	**Description**
Dependent variables	
Probability of colonisation - first and second periods	Binary variable (1,0) describing whether colonisation has occurred (1) or not (0). Colonisation is the occurrence of a species on a transect, excluding transects where it was already present.
Rate of change in abundance - first and second periods	Rate of change in the number of quadrats occupied on each transect, standardised to a rate per ten years
Rate of change in percent quadrat cover per ten years - second period only	Rate of change in mean percent quadrat cover on each transect, standardised to a rate of change per ten years
Predictor variables	
Variables that changed over time	
Oversowing	Mean ratio of abundance of oversown to non-oversown species over each time period
Tall-tussock	Mean abundance of tall-tussock (*Chionochloa* spp.) over each time period
Short-tussock	Mean abundance of short-tussock (*Festuca novae-zelandiae*) over each time period
Tenure	Whether the transect was in conservation or pastoral tenure at the initial measurement
Initial abundance Rate of change in abundance models only	Initial abundance of the species at the beginning of the period (number of quadrats per transect)
Initial percent quadrat cover Rate of change percent cover models only	Initial percent mean quadrat cover of the species at the beginning of the second period
Variables that did not change over time	
Soil acidity	Principal component 1 (see Table 2): declining log base saturation declining square-root calcium declining pH declining log potassium declining log magnesium
Declining soil fertility	Principal component 2 (see Table 2): declining cation exchange capacity declining log sodium increasing bulk density declining magnesium
Solar radiation	Amount of potential solar radiation (watts per square metre), calculated from latitude, aspect and slope (Kaufmann and Weatherred 1982)
Precipitation	Mean monthly precipitation (30 year mean), interpolated from 500×500 m resolution surfaces (mm) (Wratt et al. 2006)

Table 2: Results of the principal components analysis (PCA) for the measured soil variables. Values shown are the loadings of each variable on each of the first two axes (components).

Variable	**Loading on axis 1 (soil acidity)**	**Loading on axis 2 (declining soil fertility)**
Log soil base saturation (%)	-0.489	-0.033
Square-root soil calcium (me/100g)	-0.451	-0.180
Log soil pH	-0.401	0.237
Log soil potassium (me/100g)	-0.394	-0.206
Log soil magnesium (me/100g)	-0.360	-0.331
Soil bulk density	-0.202	0.453
Log soil phosphorus (µg/ml)	-0.157	-0.124
Log soil sulphur (ppm)	0.156	-0.267
Square-root soil cation exchange capacity	0.145	-0.503
Log soil sodium (me/100g)	0.035	-0.463
Cumulative percent variance explained	40.0	70.8

Table 3: Means (± standard errors) of elevation, mean oversowing ratio, mean ratio of exotic to native species, mean tall-tussock abundance, and mean short-tussock abundance according to tenure at the first and second measurements (beginning of first and second periods). Note that tenure at the third measurement was not used in the models.

	Measurement		
	First	**Second**	**Third**
Conservation tenure	N=16	N=31	N=41
Mean elevation (m)	1089.31 ± 80.36	1106.84 ± 45.97	1184.22 ± 41.47
Mean oversowing ratio	0.02 ± 0.01	0.03 ± 0.01	0.02 ± 0.01
Mean ratio of exotic:native species	0.30 ± 0.05	0.42 ± 0.07	0.30 ± 0.06
Mean tall-tussock abundance	29.00 ± 4.83	32.13 ± 2.92	33.32 ± 2.65
Mean short-tussock abundance	12.56 ± 4.01	9.74 ± 2.43	8.71 ± 2.10
Pastoral tenure	N=108	N=93	N=83
Mean elevation (m)	1155.37 ± 29.93	1160.13 ± 34.03	1128.70 ± 36.43
Mean oversowing ratio	0.03 ± 0.01	0.04 ± 0.01	0.04 ± 0.01
Mean ratio of exotic:native species	0.98 ± 0.31	1.36 ± 0.37	3.49 ± 2.23
Mean tall-tussock abundance	21.55 ± 1.85	21.37 ± 2.06	19.33 ± 2.13
Mean short-tussock abundance	17.50 ± 1.73	15.21 ± 1.75	16.75 ± 1.80

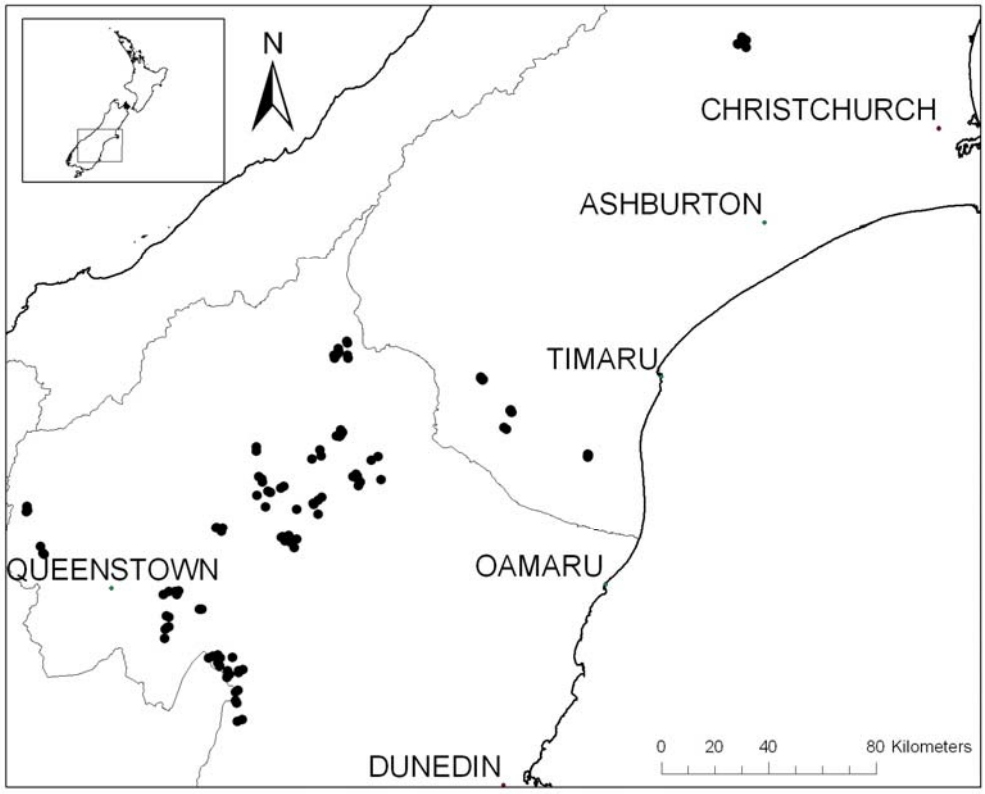


Figure 1: Locations of 125 permanently-marked tussock grassland transects in Canterbury and Otago that were measured during this study.

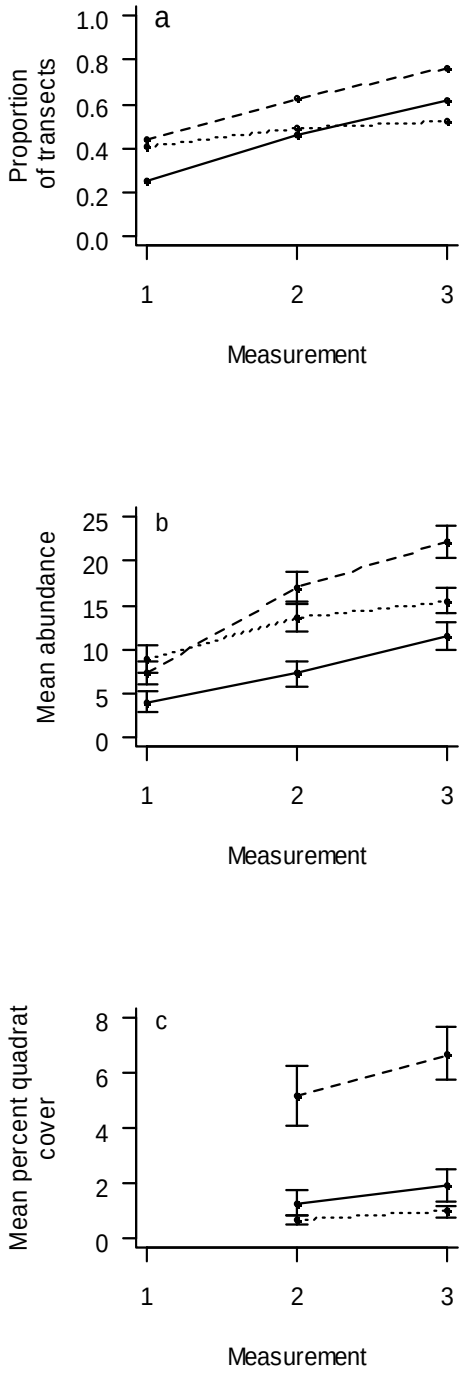


Figure 2: Change across the three measurement times in the (a) number of transects occupied out of 124, (b) mean abundance, measured as the mean number of occupied quadrats per transect for 124 transects, and (c) percent cover on 120 transects of *Hieracium lepidulum* (solid lines), *H. pilosella* (dashed lines) and *H. praealtum* (dotted lines). Error bars represent standard errors of the means. Note that four transects were omitted from the values for percent cover due to missing data at the second measurement.

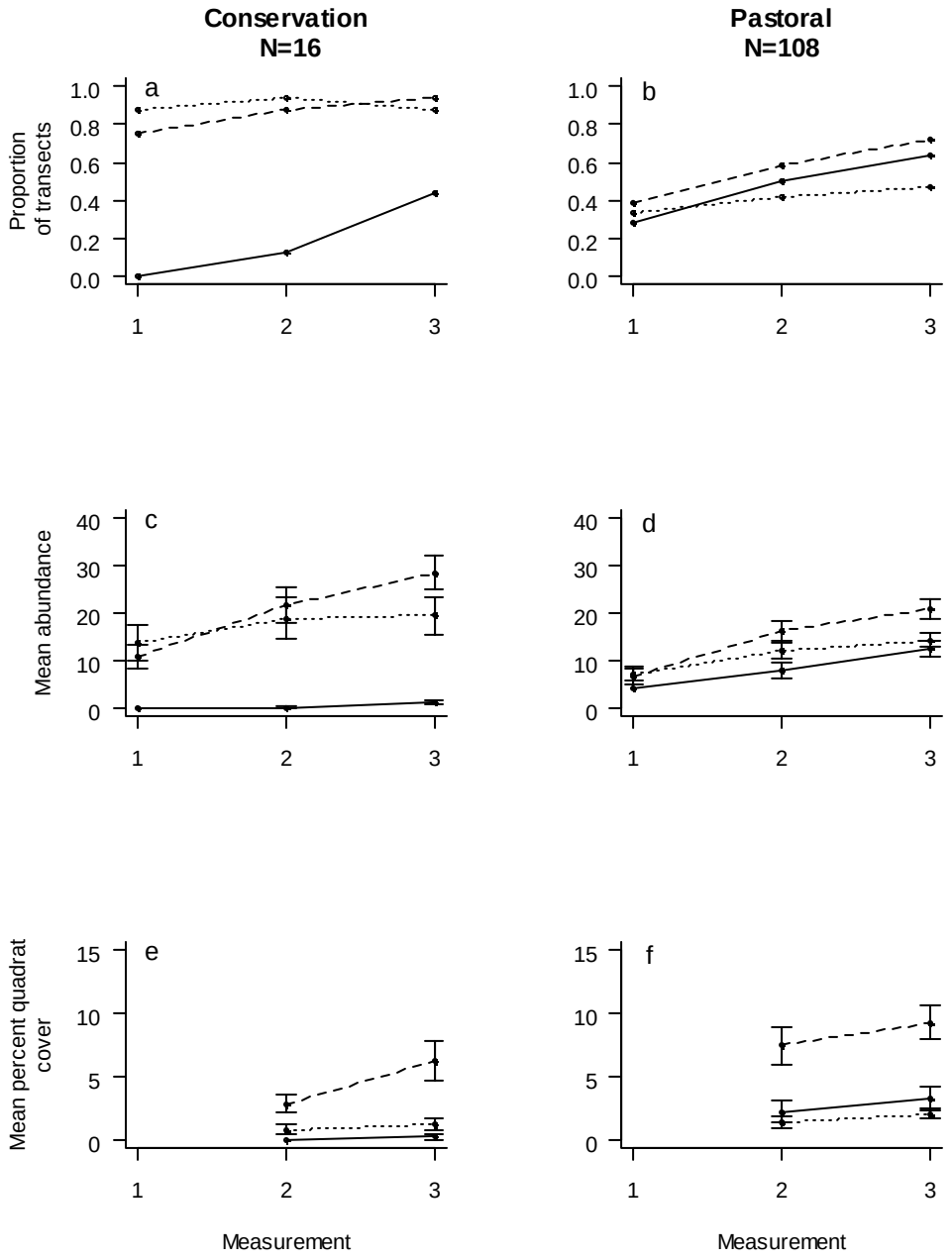


Figure 3: Change across the three measurement times for each species in the proportion of 124 transects occupied in (a) conservation tenure and (b) pastoral tenure at the first measurement. Change in mean abundance, measured as the mean number of occupied quadrats per transect on (c) conservation tenure and (d) pastoral tenure at the first measurement. Change in mean percent quadrat cover on transects in (e) conservation tenure and (e) pastoral tenure at the first measurement. *Hieracium lepidulum* (solid lines), *H. pilosella* (dashed lines) and *H. praealtum* (dotted lines). Error bars represent standard errors in the means. Note that for consistency these graphs show tenure at the first measurement so that transects that were in pastoral tenure then changed in to conservation tenure are presented in pastoral tenure at the second and third measurements. Four transects in pastoral tenure were omitted from the values for percent cover due to missing data at the second measurement.

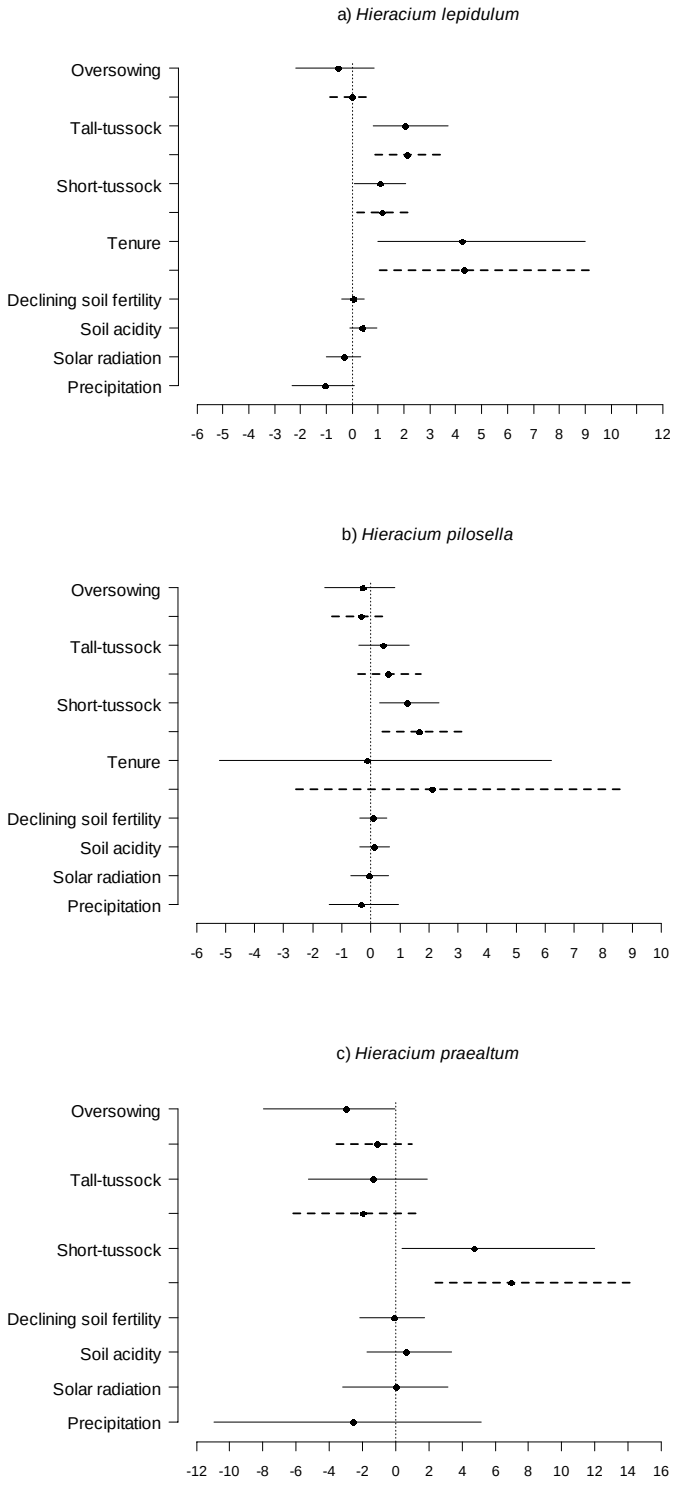


Figure 4: Estimated effects of environmental variables on the colonisation of *H. lepidulum*, *H. pilosella* and *H. praealtum*. Points represent the mean estimate, lines represent the 95% credible interval. Solid lines for oversowing, tall-tussock abundance, short-tussock abundance and tenure represent the effect during the first period, dotted lines represent the effect during the second period. Variables were considered "significant" if their credible interval did not overlap zero and marginally significant if most of the interval did not overlap zero (see methods). Tenure was not put in to the *H. praealtum* model, because it was highly unbalanced.

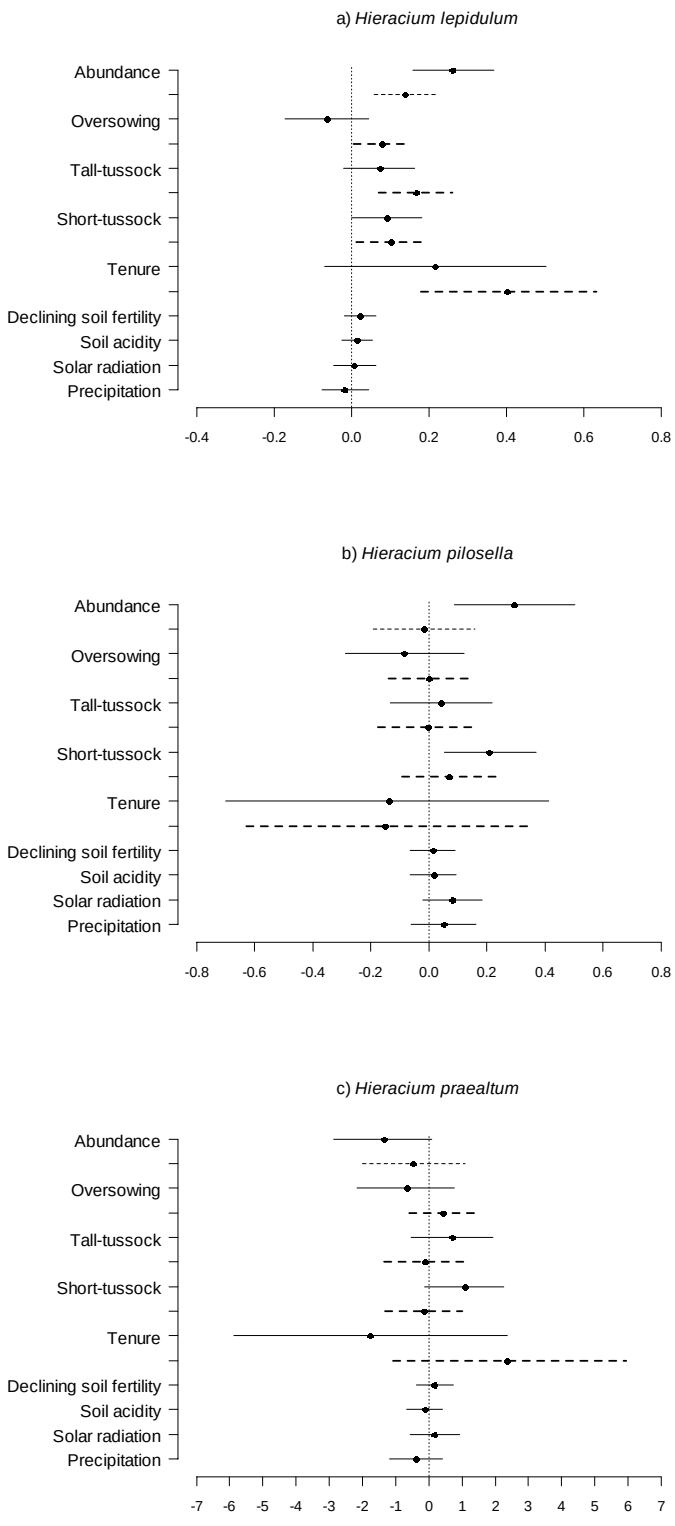


Figure 5: Estimated effects of environmental variables and initial abundance on the rate of change in abundance per 10 years of *H. lepidulum*, *H. pilosella* and *H. praealtum*. Points represent the mean estimate, lines represent the 95% credible interval. Solid lines for abundance, oversowing, tall-tussock abundance, short-tussock abundance and tenure represent the effect during the first period, dotted lines represent the effect during the second period. Variables were considered "significant" if their credible interval did not overlap zero and marginally significant if most of the interval did not overlap zero (see methods).

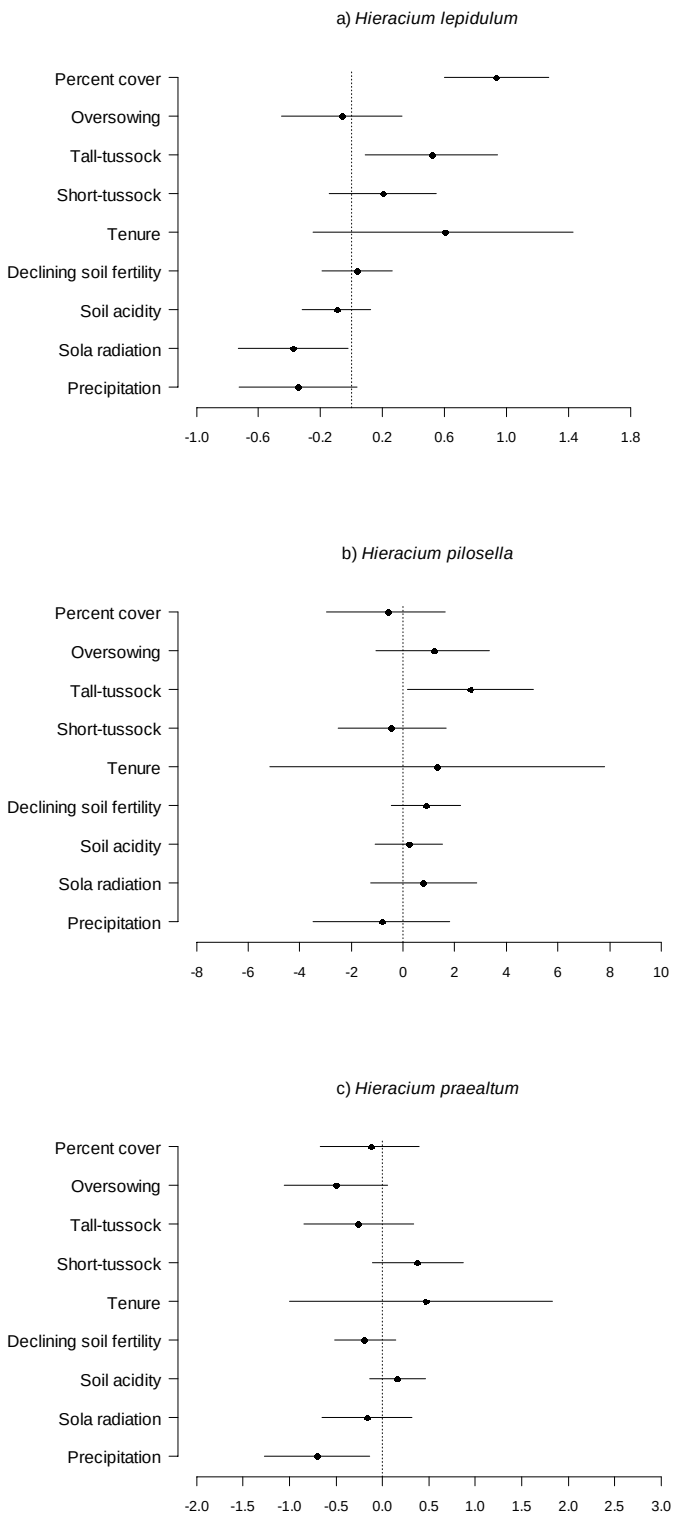
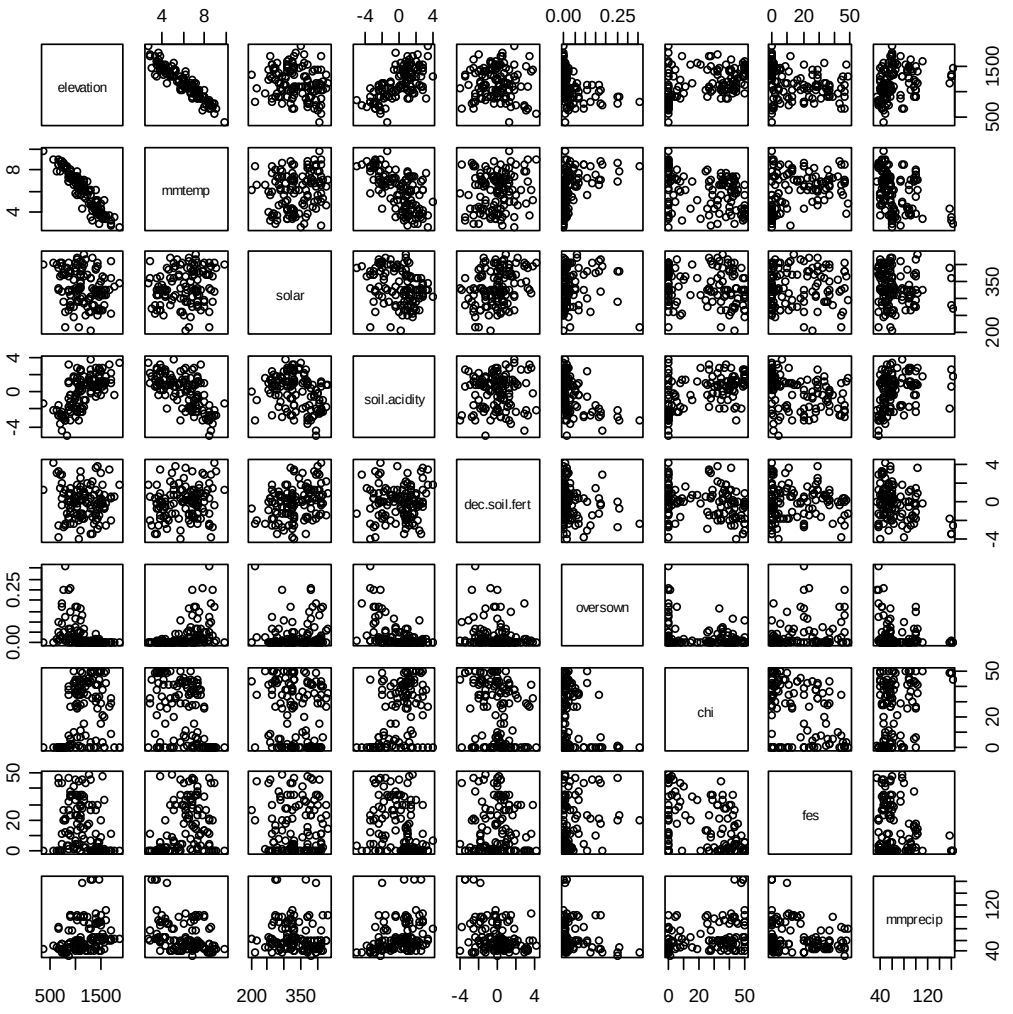
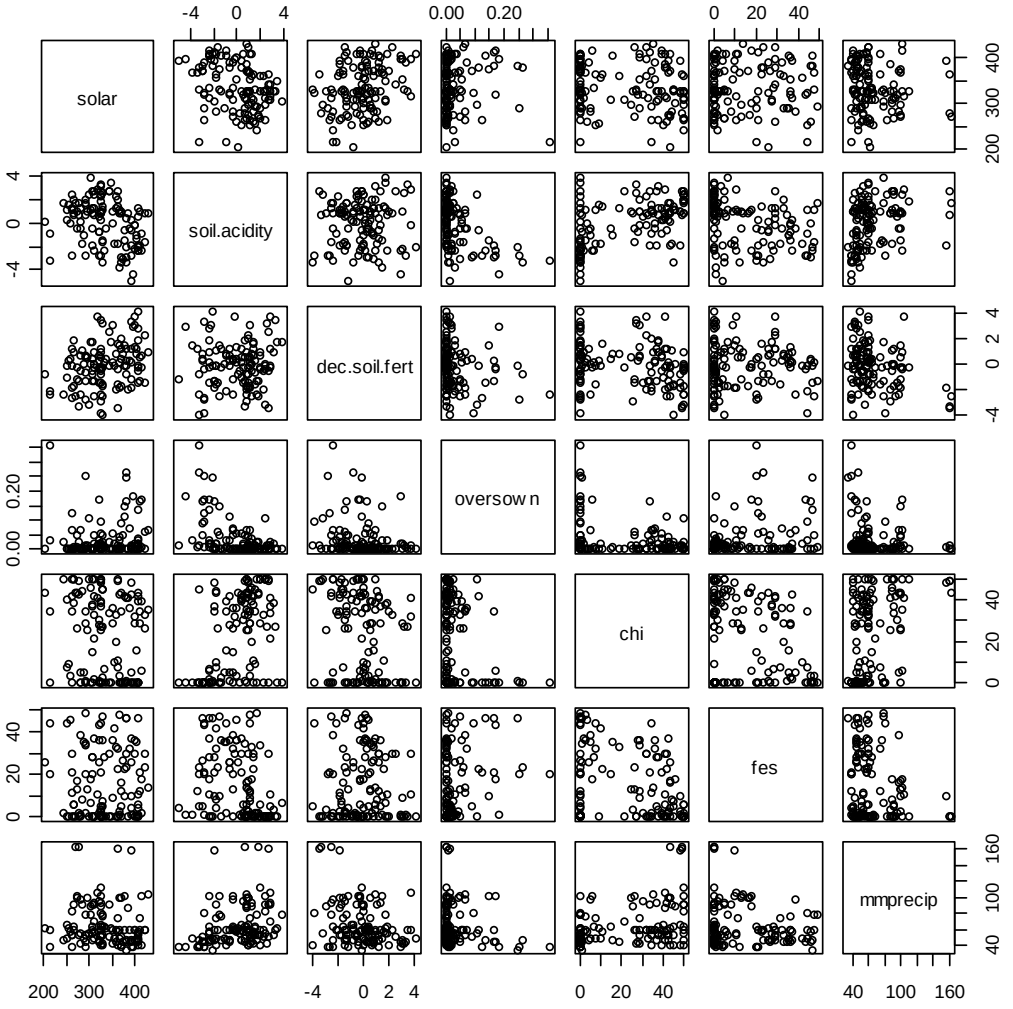


Figure 6: Estimated effects of environmental variables and initial percent cover on the rate of change in quadrat percent cover per 10 years of *H. lepidulum*, *H. pilosella* and *H. praealtum* for the second period. Points represent the mean estimate, lines represent the 95% credible interval. Variables were considered "significant" if their credible interval did not overlap zero and marginally significant if most of the interval did not overlap zero (see methods).

Appendix 1: Correlation plots between all potential explanatory environmental variables. Bare and litter are mean percent quadrat covers, oversown is the mean ratio of the abundances of oversown to not-oversown species, chi is the mean abundance of tall tussocks (*Chionochloa* spp.) and fes is the mean abundance of short-tussocks (*Festuca novae-zelandiae*) over the study. soil.acidity is soil acidity (first principal component), dec.soil.fert is decreasing soil fertility (second principal component), mmtemp is mean monthly temperature, solar is the amount of potential solar radiation, and mmprecip is the mean monthly precipitation.



Appendix 2: Correlation plots between all explanatory variables that were put in to models. Oversown is the mean ratio of the abundances of oversown to not-oversown species, chi is the mean abundance of tall tussocks (*Chionochloa* spp.) and fes is the mean abundance of short-tussocks (Festuca novae-zelandiae) over the study. soil.acidity is soil acidity (first principal component), dec.soil.fert is decreasing soil fertility (second principal component), solar is the amount of potential solar radiation, and mmprecip is the mean monthly precipitation.



Appendix 3: Correlation between tenure and rock type at each measurement.

	First measurement		Second measurement		Third measurement	
	Greywacke	Schist	Greywacke	Schist	Greywacke	Schist
Conservation	16	0	31	0	31	10
Pastoral	44	64	29	64	29	54